A COMPASS DIRECTIONAL PHENOMENON IN MUD-SNAILS AND ITS RELATION TO MAGNETISM [1]

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The tendency of the mud-snail, *Nassarius,* to veer away from an initial southward path, in the earth's magnetic field, displays both a solar-daily and a lunar-daily rhythmic component. It was demonstrated (Brown, Brett, Bennett and Barnwell, 1960; Brown, Webb and Brett, 1960) that an increase in intensity of the horizontal component of magnetic field from the earth's natural one, 0.17 gauss, to 1.5 gauss increased the veering tendency. The increased turning in response to experimentally augmented field also showed, parallelly, both solar and lunar daily variations and their derivative by periodic interference, the synodic month. The south-directed snails were able, furthermore, to distinguish between 1.5-gauss horizontal fields which were parallel to their body axis and to the earth's field and those which were at right angles to them both (Brown, Bennett and Webb, 1960; Brown, 1960).

In some preliminary experiments it was found also that *Nassarius,* while being held in a uniformly illuminated field, appeared to distinguish among the four compass orientations, north, east, south and west, and to exhibit a mean path characteristic for each of these directions (Brown and Webb, 1960). This compass-directional phenomenon seemed to possess a monthly modulation. The pattern of differences of turning for the four compass directions during the fortnight centered on full moon, in each of two consecutive months, was of large amplitude and unimodal with maximum right turning when north-directed and minimum when south-directed. For the alternate fortnights, those centered on new moon, the pattern was bimodal and of approximately half the amplitude, with maxima in right turning when either north- or south-directed and minima when east- or west-directed.

Experiments with the planarian worm, *Dugesia* (Brown, 1962a), have revealed a comparable compass-directional phenomenon with right-turning when the worms are directed either northward or southward and left-turning when directed either eastward or westward. The horizontal vector of magnetism was shown clearly to be involved in this response by experiments in which a horizontal bar magnet, producing a 5-gauss field at the level of the worms, was rotated beneath the orienting worms. The worms behaved as would have been expected

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had the apparatus itself simply been rotated in the earth's field. However, to a rotated 10-gauss horizontal field the resulting pattern was essentially the inversion, or mirror-image, of that observed for the 5-gauss and for the earth's natural one.

The following experiments were designed to determine more decisively whether mud-snails actually do exhibit such a compass-directional phenomenon in the earth's field, and if so, to learn more concerning its characteristics, including its degree of reproducibility or variability and whether it is, as proven for the worms, dependent at least in part upon response to magnetism.

Methods and Materials

Mud-snails, *Nassarius obsoletus*, were collected every few days from Chapoquoit beach on Buzzards Bay near Woods Hole, Massachusetts. The apparatus was essentially the same as that employed in the earlier published experiments (Brown, Brett, Bennett and Barnwell, 1960). There were, however, two differences. First, the visual field into which the snails emerged from their corral was, among the experiments, in some cases symmetrical and in others asymmetrical with a black background to the left and a white one to the right. Second, the sectors of the grid for recording the clockwise or counterclockwise deviations of individual snail paths at the end of three centimeters of free movement were 11.25° ones for the experiments conducted in 1961 and 1962 instead of the 22.5° ones employed in 1959 and 1960. However, as in the earlier experiments one sector was centered directly ahead of the corral exit (0°). The experimental observations consisted of ascertaining the amount of turning of snails as either the whole apparatus or, instead, simply a horizontal experimental magnetic field was rotated.

Orientation of apparatus in the earth's field. The data on the relationship between geographic direction of the snails' initial orientation and their subsequent turning tendency were obtained from four experiments. In three of these experiments series were run always in quadruplicate, involving four observers using four identically constructed pieces of apparatus. The fourth experiment was run in duplicate.

Experiment I was done during the summer of 1960 on 43 different days between June 30 and August 30. In this experiment the snails emerged from the funnel-shaped neck of their corral into a symmetrical, white field. Five snails emerged in each of the four compass directions, north, east, south, and west, and then the series was immediately repeated in the same sequence. The average path of the ten snails for each direction was determined. The observations were made always between 1:00 and 3:30 PM.

Experiments II and III were both performed during the summer of 1961. The conditions of these two experiments differed from one another and from the conditions of the 1960 experiment. The snails now emerged into an asymmetrical visual field with a black background to left and a white one to right. The mean paths of all snails in both these experiments favored clockwise turning; the snails were, on the average, positive in phototactic response.

Experiment II, totalling 17 quadruplicate series, involved two series obtained each week between June 22 and August 17, inclusive. Between June 22 and July 6 the mean path for each of the four geographic directions was obtained from series in which additional experimental variables were interpolated (for another purpose) between the successive simple directional ones. Each series comprised emergence of snails under each of 13 conditions: N-directed, two experimentally modified magnetic conditions; E-directed, the same two modified magnetic conditions; S-directed, the two modified fields; W-directed, the modified fields; and finally N-directed in a reversed asymmetrical field. For each daily series, conducted always between 1:00 and 3:30 PM, five snails were permitted to emerge from the corral under each of the 13 conditions, and then, immediately, five snails emerged under each of the 13 conditions in the reversed order of the series. From these series the values obtained for the N-, E-, S- and W-directed samples were isolated and used in the analysis presented in this report. From July 11 through August 17, the series was simplified to the four compass directions alone, with five snails emerging in each of the four directions in a clockwise order (N, E, S and W); then, at once, the series was repeated in the reversed order. As with Experiment I these data were reduced immediately to the mean path for the samples of 10 snails for each direction. The data obtained after July 10 appeared to yield a pattern consistent with those obtained for the period before this date.

Experiment III comprised 25 quadruplicate series obtained during the period of June 21 through August 18, usually on three days of each week. A series consisted of recording five snail-paths under each of a sequence of 14 conditions and, at once, the paths of five snails under the same conditions but in reversed order. Again, the experiment was conducted always between 1:00 and 3:30 PM. The conditions in this group and their serial order were: N, NE, E, SE, S, SW, W, NW and five magnetically modified fields followed by a N-directed, reversed asymmetrical visual field. The last six conditions were included for another purpose. From this series the results obtained for the N-, E-, S- and W-oriented samples were isolated and treated separately for comparison with the data from Experiments I and II. However, the data of all eight compass directions were also analyzed as a unit, and the results were compared with those of a later experiment employing the same eight directions.

Experiment IV comprised directional observations made in 1962 in association with a study of response to alterations in electrostatic fields. Series were run on 27 afternoons between June 20 and August 17, inclusive. Two observers each recorded the paths of five snails for each direction as the apparatus was rotated from N to NE to E to SE. For each direction the snails were subjected first to equipotential plates to right and left followed by a 2-volt/cm. gradient in the air with the positive plate first to right and then to left. The order of the last two conditions was alternated from one series to the next. Immediately upon completion of the series, the order was traversed in the reverse sequence, again with five snails for each condition. Meanwhile two other observers were carrying out observations with fully comparable series but for the directions S to SW to W to NW, and the reverse. From these series the mean paths for each of the four directions, N, E, W and S, with the equipotential fields were isolated and compared with the data for the preceding two summers. The data for the entire eight directions were also considered in comparison with those eight obtained in 1961.

Rotation of an experimental horizontal magnetic field. In a second kind of experiment, V, snails were observed as they emerged from the corral in apparatus oriented so that the organisms always moved initially north but with different orientations of an experimental, horizontal magnetic field. This experiment was always performed by four observers working concurrently with four sets of apparatus. A total of 26 quadruplicate series were recorded between June 21 and August 18, 1961. The series were always obtained in the morning between 8:30 and 11:00, three days a week. Each experimental series comprised recording the path of snails in a series of conditions as follows: (1) controls in the earth's natural field, (2) horizontal experimental 5-gauss fields with S-pole of the bar magnet directed in each of eight compass directions. The sequence in the series was on each occasion as follows: (1) control; (2) 0° (N); (3) 45° (NE); (4) control; (5) 90° (E); (6) 135° (SE); (7) control; (8) 180° (S); (9) 225° (SW); (10) control; (11) 270° (W); (12) 315° (NW); and (13) control. The paths of five snails were determined for each condition from 1 through 13, and then, after assaying the paths of 10 snails in a reversed asymmetrical field, passing back through the series from 13 to 1. By this procedure, controls in the two-way series both immediately preceded and followed each experimental magnetic orientation. The mean path of the 10 snails for each experimental condition was then determined and expressed as the difference from the mean of all control paths.

A double experiment: Rotation of apparatus and rotation of 5-gauss field. Additional experiments were done during mornings of 1962 from June 21 through August 18. One of these, Experiment VI, resembled Experiment IV except that it was conducted between the hours of 8:30 and 11:00 AM instead of 1:00 and 3:30 PM. Twenty-six duplicate series of 8 compass directions were thus obtained by four observers working concurrently and cooperatively. On alternate mornings, similarly usually three days a week, 26 quadruplicate series (Experiment VII), were obtained as follows. The snails were always directed magnetic north but were subjected, *in shuffled order*, to 16 conditions. Twelve of these involved horizontal fields of 5 gauss with the south pole of the bar magnet oriented in 12 compass directions; for the remaining four conditions the experimental field was removed completely so as to provide controls in the earth's field. The twelve directions of the 5-gauss field were 0°, 22.5°, 45°, 67.5°, 90°, 112.5°, 135°, 157.5°, 180°, 225°, 270° and 315°. As in other series, the 16 conditions were assayed by five snail paths first in one order and then in reversed order. The mean path for each of the compass orientations was then expressed as the difference from the average path for all controls in the same series.

Results

I. *Apparatus rotation in the earth's field*

a. *Four compass directions.* The relationship between turning tendency of snails during the first three centimeters of free movement after emergence from a corral exit and the compass direction in which the exit was directed was determined in the following manner from the data of the afternoon experiments I for 1960, II and III for 1961, and IV for 1962 and the morning group VI for 1962. The mean path of all snails for the two or four replicate series for the particular afternoon or morning for all four or eight directions was first determined. Then the mean path for each of the four directions, N, E, S and W, was expressed as the difference from the mean path for all the directions. The average differences for all the series in each experiment are plotted separately in Figure 1.

For experiments I, II and III a general similarity is evident both in form

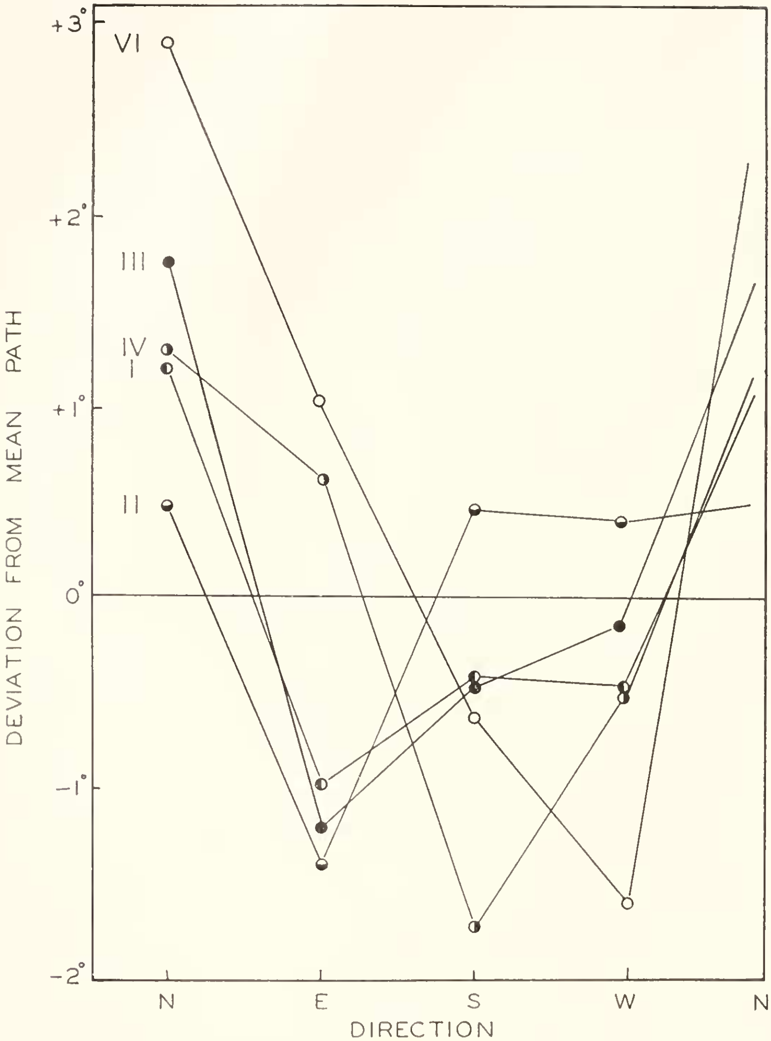

FIGURE 1. The variation in mean path of snails, in a uniform pattern of illumination, with the compass direction of the initial path. Roman numerals refer to the experiments described in the text.

and amplitude in the variation in mean path with compass direction. This is true whether the mean path of all the snails averaged close to 0°, as in the symmetrical fields employed in 1960, or averaged about +16°, as in the asymmetrical fields employed in 1961. However, the form of the compass relationships for the 1962 snails of Experiment IV, obtained at the same time of day as the earlier group but in the equipotential fields in the morning, differed somewhat from those seen for Experiments I, II and III.

When the differences between paths for the E-directed and N-directed snails were examined, a non-parametric comparison of the 43 samples of Experiment I revealed 28 negative, 14 positive and 1 zero ($P < 0.05$). A similar comparison for Experiment II yielded 12 negative and 5 positive ($P < 0.1$), and for Experiment III 18 negative, 4 positive and 3 zero ($P < 0.005$). A non-parametric consideration of the combined experiments (58 negative, 23 positive, 5 zero) yielded $X = 15.1$; $P < 0.001$. For the N to S difference for Experiment IV there were found 28 negative, 22 positive and 2 zero. For experiment VI the N to W difference showed 34 positive, 17 negative and 1 zero ($P < 0.02$).

b. *Monthly rhythms in north-to-east path difference.* Despite substantial variability within each of the four afternoon groups there appeared to be a reasonably reproducible, significant mean compass-directional response for the snails in the earth's natural field. In view of the preliminary suggestion that this directional phenomenon displayed a monthly variation (Brown and Webb, 1960), the data were examined for the existence of such a periodism. The differences between the paths of E- and N-directed snails for Experiments I, II and III are plotted against calendar date in Figure 2A. The calendar dates for 1960 have been displaced along the abscissa, relative to those for 1961, in order that the three groups be phase-synchronized with respect to elongation of the moon. The days of new moon are indicated.

It is evident from inspection of Figure 2A that a large measure of the observed variability in the relationship between compass direction and snail path is attributable to a synodic monthly variation. The large N to E difference illustrated in Figure 1 for 1960 and 1961 is most striking for the periods over full moon and least so for the periods over new moon. At this latter time there is an evident tendency for this directional relationship even to reverse sign. Eighteen of the 23 cases of the reversal indicated earlier are seen to be accounted for during 15-day periods centered on new moon.

It is also noteworthy that in passing from late June and early July to late August there is for each of these two years a gradual trend toward reduction in amplitude of the directional phenomenon. The data also suggest that when the effect is strongest, as in early summer, there is a tendency for (1) assumption of a semi-monthly variation, and (2) occasional single-day inversions, *e.g.*, July 14 and 19, 1960. Such abrupt inversions appear conspicuously to be followed the succeeding day by unusually strong effects in the more typical direction for the period.

An examination of the corresponding parameter for the data of Experiment IV, obtained at the same time of day, but in 1962, revealed that there was not a monthly but rather a semi-monthly variation in the north to east difference. This variation is illustrated in Figure 2B where the path of the east-directed, relative to the north-directed snails, is plotted in relation to the days of both new and full moons for the two-month period. The data illustrated in Figure 2B include all 27 days investigated in 1962. The data were rather uniformly distributed over four consecutive semi-months of the summer. For the first semi-month there were 7 days of data, ranging from 11 days before new moon to three days afterward. For the second semi-month there were also 7 days, ranging from 11 days before full moon to three days afterward. The third semi-month included 7 days, ranging from 8 days before new moon to three days afterward, and the fourth semi-month contained 6 days, ranging from 9 days before full moon to two days afterward.

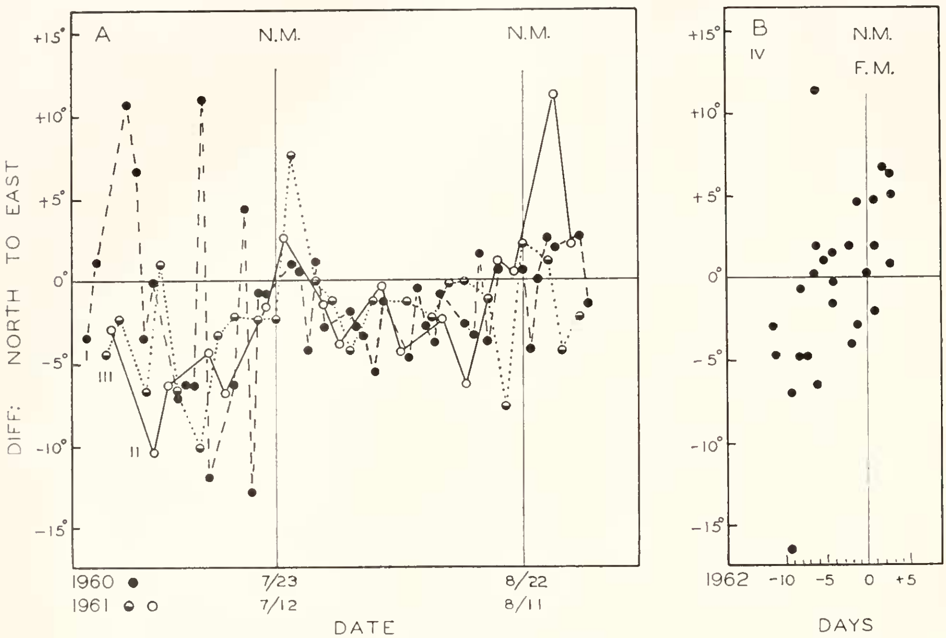

FIGURE 2. A. The variation in difference between the mean paths of E-directed snails and N-directed ones with calendar date for one experiment, I, in 1960 and two independent experiments, II and III, in 1961. B. The comparable differences for the two-month series of experiment IV conducted in the summer of 1962, with the values now plotted with reference to days of new and full moon.

The relationship changed sign over new moon in 1962 just as it did for the preceding two summers, but now, in addition, there was sign reversal over the time of full moon. The two highly anomalous values in Figure 2B were obtained on June 22 and 25, 6 and 9 days before the early-summer new moon, a period when comparable highly atypical values were obtained during summer of 1960.

c. *Eight compass directions.* It will be recalled that the series of Experiment III, involving rotation of snails in the earth's field alone, included compass directions not only parallel (N and S) and at right angles (E and W) to the horizontal vector of the geomagnetic field, but also directions 45° from these (NE, SE, SW, NW). It is seen in Figure 3A, in which the mean path is plotted against compass direction, that the paths of snails for which magnetic direction deviates by 45° from a parallel or right-angle relationship are in every instance observed to be further to the left than for the adjacent parallel or right-angle fields. It will be noted that the mean paths for all the directions involved right-turning because of the asymmetrical field in 1961.

A quantitative analysis involving all 100 values disclosed the mean path for the directions, NE, SE, SW and NW, to average 1.103° to the left of the mean

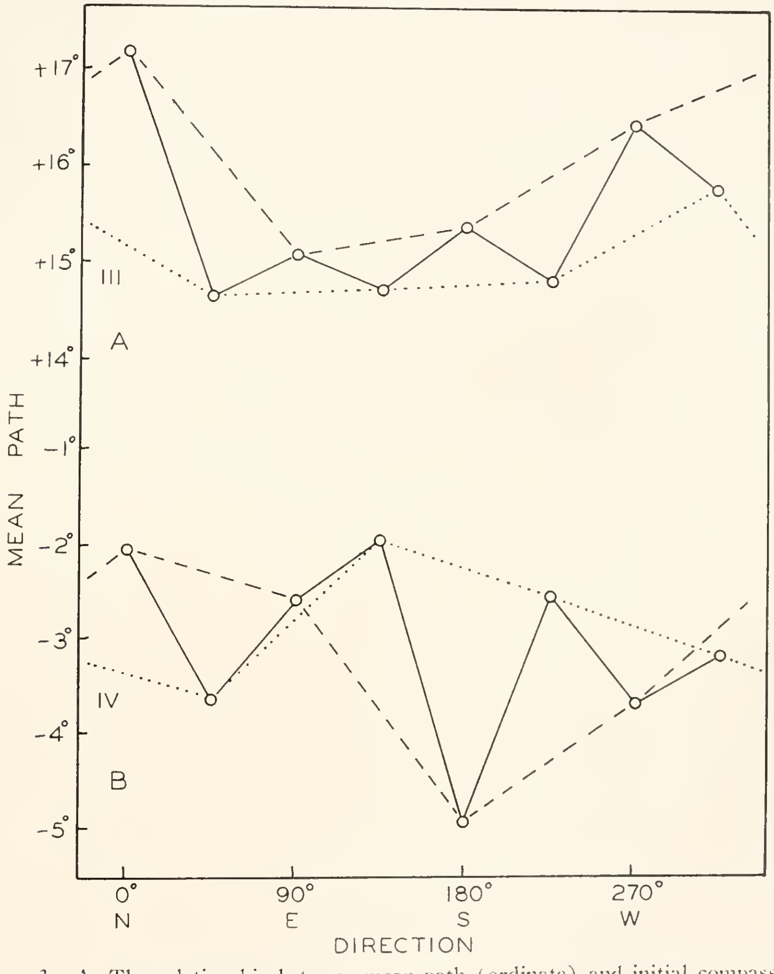

FIGURE 3. A. The relationship between mean path (ordinate) and initial compass direction (abscissa). Snails moved in an asymmetrical light field with a black background to their left. Ordinate values are expressed as deviations from zero which, in turn, represents the direction of initial path. Dashed lines connect the set of points at N, E, S and W; dotted lines connect the set of points for NE, SE, SW and NW. The paths taken for the latter set of directions lie consistently to the left of those taken for the former. B. The comparable relationships in a symmetrical light field and with an artificially produced right-left symmetry of electrostatic field. Note the inversion of relationship between sets of points as initial direction changes from N to SE.

path obtaining for the adjacent directions N, E, S and W. The standard error of the difference was not exactly the same when one computed the differences in paths from those in the adjacent parallel or right angle fields in a clockwise direction on the compass dial as when one computed them from the adjacent ones in a counterclockwise direction. These were ±0.332 and ±0.350, respectively, with $N = 100$. This yielded in either case, however, $P < 0.003$. It seems evident, therefore, that the snails, as indicated by their response, distinguished between parallel or right-angle orientations to the earth's magnetic axis and orientations deviating 45° from these.

When a comparable study was made for all eight directions during two months of the summer of 1962 (Exp. IV) at the same time of day (Fig. 3B) all the comparable relationships appeared to be reversed except for the north to NE and N to NW ones. The mean paths for the SE and SW directions, in consequence, appeared similar to the path for north. The only known and controlled differences between the conditions of the 1961 experimental series shown in Figure 3A and of the 1962 series of Figure 3B were that the field of emergence (1) was asymmetrical in 1961 and symmetrical in 1962, and (2) included the natural ambient electrostatic right-left gradients in 1961 and an experimental equipotential right-left one in 1962. It is interesting that despite the symmetrical field, the mean paths for all directions in 1962 favored slight left turning.

II. *Rotation of a 5-gauss field*

The effect of rotation of a 5-gauss horizontal experimental field (Exp. V, 1961) was determined by computing for each day the mean path of the 40 snails of the quadruplicate sample for each compass direction of orientation of the south pole of the magnet and expressing these as deviations from the mean path for the 200 control snails in the series of the same day. In comparison with the compass directional phenomenon in the earth's natural field, directing the south pole of the bar magnet to the east was the magnetic directional equivalent for the snails of being westbound in the earth's field, and directing the south pole to the west was the magnetic equivalent of a natural eastward path. In other words, clockwise rotation of the experimental magnetic field is the magnetic equivalent for the organism of counterclockwise rotation of the apparatus in the earth's field.

In Figure 4A is plotted the mean path of the snails for each of the magnetically simulated geographic directions, expressed as path difference from all controls in the same series. In the same figure are seen the results for Experiments I and II of rotation of the snails in the earth's field alone. The relationship of response to magnetically simulated direction is seen to approximate closely an inversion of the comparable relationship for the earth's field. Just as for the natural compass-directional phenomenon, the largest difference occurs between N and E, or between the N-directed and W-directed 5-gauss experimental fields. The difference in paths between N and E equivalent magnetic orientations was found to be 1.245 ± 0.385° ($t = 3.23$; $N = 26$, $P < 0.005$).

Experiments VI and VIII were fully independent ones, performed on alternating mornings of the week. Here it is possible to compare for the same time of day for the same two-month period the results of rotating the apparatus in the earth's field with the results of rotating a 5-gauss horizontal experimental magnetic field to simulate the geographical rotation. Both experimental series were similar, too, in being obtained in an equipotential, right-left field across the organism. The two series differed, however, in that the compass directional study was one of an orderly clockwise and then counterclockwise rotation while the experimental magnetic orientations were presented in shuffled order.

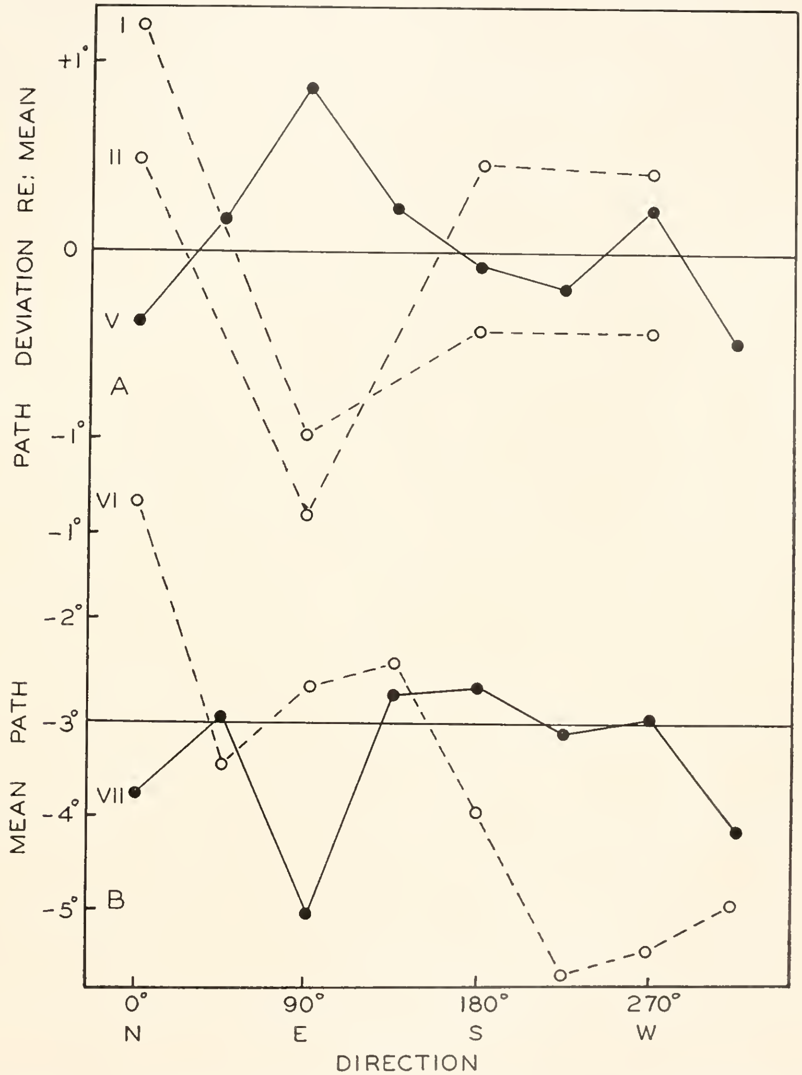

Figure 4. A. Comparison of the pattern of path variation with compass rotation of the initial path in the earth's field, experiments I and II (broken line), and with rotation of a 5-gauss horizontal field, experiment V (solid line), in the opposite direction. B. Same as in A, experiment VI (broken line) and experiment VII (solid line). See text for experimental conditions.

In Figure 4B the mean snail-paths are plotted as a function of both compass direction in the earth's field, and of rotation of a 5-gauss field while the snails were directed steadily northward. The values for the experimental magnetic fields have been plotted as the simulated compass directions as for Figure 4A.

It is evident from Figure 4B that just as had been seen for the experiments in 1961, the snails appeared to be responding to the rotating 5-gauss magnetic field but were exhibiting a response of slightly lower amplitude and in the opposite direction to that observed for the snails during the same period in the earth's 0.17-gauss field. This opposite relationship between response to the natural and the artificial fields obtained for both years, therefore, despite the fact that the

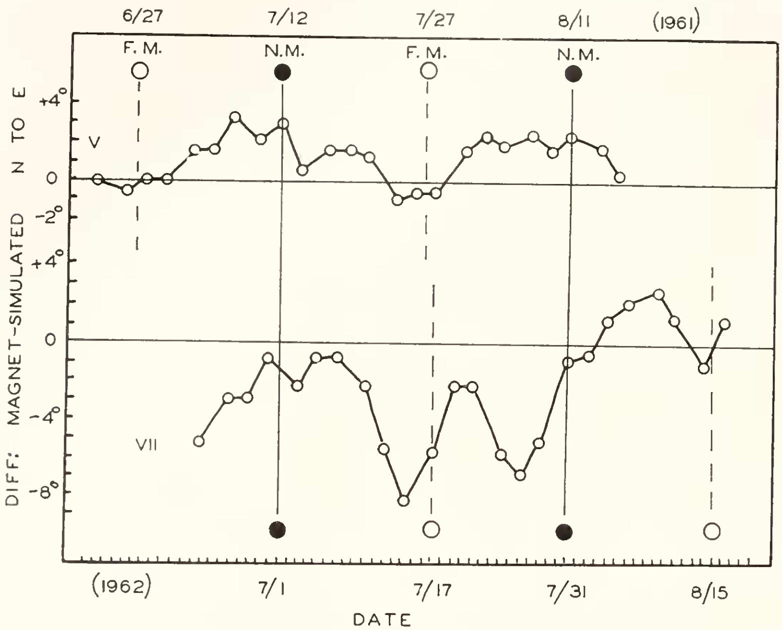

FIGURE 5. Three-day (= weekly) moving means of the difference of the mean path of N-directed snails when in a W-directed 5-gauss field (simulated geographic east) from path with the 5-gauss field N-directed for experiment V in 1961 (upper curve) and for experiment VII in 1962 (lower curve).

two-month periods of 1961 and 1962, with their differing experimental conditions and times, each had its own characteristic associated compass directional pattern.

As in the case of rotation in the earth's field, substantial variability was encountered in the response to the various compass orientations of the 5-gauss field. It will be recalled that a large portion of the variability in the compass-directional behavior was accountable in terms of monthly or semi-monthly variations. If the snails were using, at least in part, the earth's magnetic field in the directional response, as is strongly suggested by the correlations depicted in Figure 4, it seemed probable that a monthly variation would also be evident for the response to the 5-gauss experimental field. Consequently, the mean path in the east-simulated 5-gauss field was expressed as difference from mean path in the north-directed one.

This gave the 5-gauss counterpart of the N to E difference in the earth's 0.17-gauss field, which was shown in Figure 2 to display a monthly or semi-monthly variation.

In Figure 5 the N to E path differences for the 5-gauss simulated field are plotted together, each expressed as a three-day (= weekly) moving mean to smooth the systematic variations, evident by inspection, in the single-day data. The dates for the two summers have been adjusted to bring into synchrony the days of new moon. The figure reveals a monthly variation for the 1961 experiment of roughly the same general character as that found for the N to E difference in the earth's field alone for the same year (Fig. 2A). A maximum in right-turning tends to center over the time of new moon and minimum over full moon. For 1962 there appears to be a semi-monthly variation as in the compass response in the earth's field for the same year (Fig. 2B). Also quite noteworthy is the relatively small amplitude of the monthly rhythm of 1961 and the much larger amplitude of the semi-monthly one of 1962, holding parallelly for both the orientation in the earth's field and in the 5-gauss simulated fields.

d. *Differences in compass directional pattern with time of day.* Experiments IV and VI, performed in exactly the same manner under the same conditions except for the difference in time of day, permit a comparison of the two to learn whether differences in compass response pattern occur with differing times of day. The morning and afternoon results for the four principal compass directions, plotted together in Figure 1, may be compared. The amplitude and overall gross character of the directional pattern are somewhat similar for the two times of day. However, a difference between them is suggested although the difference is not statistically significant with the available data. Maximum left-turning occurs for the south-directed snails in the morning and for the west-directed ones in the afternoon. That this appears to constitute an alteration in the form of the pattern rather than a phase difference is indicated by the fact that maximum right-turning at both times of day occurs for the north-directed snails.

Discussion

The compass-directional phenomenon clearly indicates a directional heterogeneity in the horizontal plane in which the snails are free to move. It indicates further that the snails must be sensitive to this heterogeneity. The modification of this response by a bar magnet suggests that geomagnetism is involved as one contributing physical factor.

One way to account for the monthly and semi-monthly variations in the directional phenomenon would be to postulate that the two-dimensional pattern of the ambient physical field that the snails perceive is systematically varying in a manner correlated with the rotation of the earth relative to the moon. Alternatively it can be postulated that the lunar rhythms in the directional phenomenon do not depend on monthly variations in particular two-dimensional physical field components by which the organism distinguishes compass directions; instead they may depend on monthly variations in the organism's response to a relatively fixed field pattern. In the latter case the organismic variation could result from a monthly variation in some other physical parameter in the pervasive geophysical environment. The latter factor could even exhibit its variability nondirectionally. Indeed, there could conceivably be an autonomous monthly oscillation within the organism. However if the last were true the phase angle of the autonomous oscillation must be precisely set by some physical variation correlated with the lunar day, such as illumination or ocean tidal events. This is necessary since for three consecutive summers the monthly orientation rhythm bore fully comparable phase-angle relations to the natural lunar month despite the differing calendar dates for these events.

Regardless of the nature of this cycle timer, the evidence suggests that the factor which determines the phases of the monthly rhythm is related to the 24.8 hour lunar day rather than to the 12.4-hour period of the ocean tides. This seems probable because a tide-correlated factor at Woods Hole, Mass., where the two tides of the lunar day are essentially equal, would be expected to produce semi-monthly rather than monthly cycles. It is difficult to see how a factor cycling every 14.8 days can synchronize a 29.5-day biological cycle with a 29.5-day environmental cycle without 180° phase differences. If, however, tides were actually phasing a monthly cycle, then for 1960 and 1961 the cycles might have been expected to be about 180° out of phase with one another. This is because in 1960 a noon high tide occurred on July 29 six days after a new moon, and in 1961 only three calendar days away on August 1, five days after a full moon. The phase-synchrony of the cycles illustrated in Figure 2A appears therefore to involve some more direct means of lunar synchrony.

In 1962, on August 6, the noon high tide occurred as in 1960, six days after a new moon, and yet the monthly rhythm did not resemble that observed for 1960 despite the repetition of the tidal relationship to elongation of the moon.

It is possible that the monthly phase relations are set solely by monthly variations in nocturnal illumination. More probable, however, would appear to be a response of the snails to some regular variation in the earth's patterns of subtle geophysical forces related to the lunar day. In support of this last hypothesis are the recently demonstrated extraordinary sensitivities of living things to the strengths and vector directions of the earth's magnetic (Brown, 1962a), electric (Brown, 1962b) and radiation (Brown, 1963) fields. Pointing to this, also, are the persistent monthly rhythms, locked in a similar lunar relationship in the flatworm, *Dugesia*, coming from a tideless habitat and held in environments with no access to nocturnal illumination. In the worms, orientational responses appear distinctly phase-synchronized to upper, or both upper and lower, transit of the moon, just as for the snails.

Supporting an hypothesis that different physical parameters are responsible for the two phenomena, (1) distinguishing compass direction and (2) monthly variation in the response to directions, are the observed results of rotating an experimental 5-gauss field, together with the monthly rhythms in response to this stronger field. The phases of the monthly rhythms are essentially synchronized for the two field strengths despite the fact the compass response patterns are the opposite of one another.

It should be emphasized, however, that this particular monthly variation of the snails cannot be attributed exclusively to a completely autonomous monthly periodism of this frequency within the organism. The expression of the rhythm is a function of arbitrarily imposed geographical or experimental magnetic directional changes on the organisms. In other words, the phase angle of one of the two essential components in the rhythm is arbitrarily, and for all practical purposes randomly, presented in time.

The mirror-image relationship that the compass response to the 5-gauss field bears to the comparable response to the earth's field suggests that there is a sign change in the response. Such a sign change has been reported for the planarian, *Dugesia* (Brown, 1962a), but in this latter instance the change occurred between 5 and 10 gauss. For *Nassarius* the sign change must occur at some field strength below 5 gauss.

One additional consideration should be mentioned at this time. This pertains to the relatively large variability in the snail responses. There is reason to believe that this resides chiefly in behavioral variability within and among individuals. This is suggested by the relatively huge variances which are encountered in the sampling for any given experimental condition and time on the one hand, and the relatively orderly and systematic variations in the means about which the individual paths vary. This is the kind of a picture one would expect to encounter if, for example, a rather poor marksman were shooting at a bullseye while the target itself was being gradually and systematically changed in its location. In view of the large variability which characterizes biological phenomena, particularly at the organismic level, it seems most reasonable at present to assume that the physical environmental factors which singly or collectively are involved in these phenomena exhibit less variability than suggested by the responses. If the biological phenomenon in this particular case were adaptive rather than probably non-adaptive, variability would be expected to be vastly reduced.

Irrespective of what factors are responsible for the monthly variation in directional response, this study does provide a fairly strong case for geomagnetism as being the most important single physical force responsible for the two-dimensional heterogeneity used as the basic reference in the compass-directional behavior described in this report. But equally supported is the conclusion that other uncontrolled geophysical variables are capable of influencing greatly the response of the organism to the relatively stable average direction and strength of this magnetic field.

Summary

1. Mud-snails in a uniform field of all ordinarily controlled directional factors distinguish among geographic directions.

2. Geomagnetism is involved in this directional sense. This was shown by rotation of a 5-gauss horizontal magnetic field which produced an orientational behavior correlated with that observed when the snails were rotated in the opposite direction in the earth's field.

3. The response pattern to compass directions of the 5-gauss horizontal field was essentially the mirror-image of that observed for the earth's 0.17-gauss field.

4. The directional response of the snails in the geographic field, and the concurrent correlated response to a rotating experimental magnetic field, vary parallelly with time and with influence of other, still undefined factors.

5. Rotation of a 5-gauss horizontal magnetic field through the series of four compass directions, differing by 45° from the four cardinal directions, may produce

a pattern of compass-directional behavior either paralleling or mirror-imaging that observed concurrently for the four cardinal directions.

6. The compass-directional pattern of response of the snails shows a monthly or a semi-monthly variation related to moon phase. There is reason to believe that this is related to the moon through some mediator other than the ocean tides or nocturnal illumination.

7. The compass-directional response to a rotating 5-gauss horizontal magnetic field, shows a monthly variation or a semi-monthly one. Whether it is monthly or semi-monthly, and its amplitude, appear to vary parallelly with comparable cycles obtained during the same period in response to equivalent changes in orientation in the earth's 0.17-gauss field. This gives additional support to the conclusion that geomagnetism plays an important role in these orientational phenomena of the snails.

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